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Fish length exclusively determines sexual maturation in the European whitefish *Coregonus lavaretus* species complex

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Author´s contributions

H.F., R.M., and U.D. designed the research. H.G. provided field data. H.F. and R.M. carried out the data analysis and model investigation, and drafted the manuscript. H.G., J.W., and U.D. critically revised the manuscript, and all authors approved its final version.

Competing interests

We have no competing interests.

Abstract

Steadily increasing water temperatures are likely to affect whitefish stocks in the Alpine lakes. The question arises whether stock management can be adapted to mitigate the consequences of this climatic change. Here, we estimate the effects of increasing water temperatures and different stocking strategies on fisheries yield by recreational anglers. Using a process-based population model based on an empirical long-term data set for the whitefish population (*Coregonus lavaretus* (L.) species complex) of Lake Irrsee, Austria, we project density-dependent and temperature-dependent population growth and compare established stock enhancement strategies to alternative stocking strategies under the aspect of increasing habitat temperatures and cost neutrality. Additionally, we contrast the results obtained from the process-based model to the results from simple regression models and argue that the latter show qualitative inadequacies in projecting catch with rising temperatures. Our results indicate that increasing habitat temperatures reduce population biomass and catch by the fishery through their effect on growth and survival. Regarding stocking strategies, we find that stocking mostly small fish produces higher population biomass than stocking mostly larger fish, while catch remains almost constant. Under warmer conditions, however, catch is maximized when mostly larger fish are stocked. For this reason, stocking larger fish seems to be more beneficial for the angling fishery under the aspect of increasing temperatures. Adaption to climate change by changing stocking strategies cannot, however, prevent an overall reduction in catch and population size.

Keywords: growth probability, natural mortality, matrix model, stocking assessment

Introduction

Compared to lakes in lowland areas, lakes in Alpine areas are typically characterized by great depth and low water temperatures [1]. Mean temperatures of surface and deepwater layers in Alpine lakes of Central Europe have, however, increased between 0.5 ℃ and 1 ℃ over the last 40 years and further warming is expected because of ongoing climatic changes [1–4]. This change in the thermal regime is very likely to affect population dynamics of fish species that are living in Alpine lake ecosystems, and consequently also the related fishery could be affected [5,6].

The planktivorous European whitefish (*Coregonus lavaretus* (L. 1758) species complex) lives in the cold-water layers of Alpine lakes and was exploited mainly by commercial fisheries before the 1970s. With improving angling techniques over the last decades, whitefish has become also very important for recreational fisheries.

To compensate for harvesting by fisheries, managers of exploited whitefish populations commonly conduct stocking programs. In general, stocking strategies comprise introductions of small (e.g., larvae) and large (e.g., one-summer-old) whitefish in various proportions. Stocking small fish is common, although many authors argue that stocking larger fish is more profitable for whitefish fisheries compared to stocking smaller fish [7–10].

Stocking strategies are almost never systematically evaluated in small fisheries [11,12]. Fisheries managers often do not pay enough attention to the cost-effectiveness of the applied stocking program and to possible negative impacts of stocking due to, e.g., density-dependent effects on growth and mortality [12,13]. Moreover, in the context of climate change, the question arises how stocking strategies can be adapted to ensure sustainable fisheries management of coldwater fish under increasing habitat temperatures.

In general, fish are poikilothermic animals and live in specific temperature ranges, preferring water temperatures that promote optimal growth [14–16]. Growth in turn is related to natural mortality [17,18,19]. Fishery yield depends on how well the fish grow and survive. Therefore, a correlation between water temperatures and catches often exist [20–23].

Mathematical models are very helpful to estimate how increasing temperatures and various stocking strategies will affect whitefish population dynamics and the related catch by the fishery. Simple regression models, fitted to observed water temperatures and catches, can be used to extrapolate catches under higher temperatures. This model approach, however, does not account for the relevant life-history processes and the resulting population dynamics.

In contrast, a process-based model approach provides additional opportunities for analyzing population dynamics and can readily be extended to account for relevant mechanisms, such as fishing, stocking, and density dependence. Models based on life-history processes are differential equations, matrix models (MMs), and individual-based models (IBMs).

Differential equations can be analytically solved for unstructured populations, while only numerical solutions are feasible (and effectively become matrix models) for structured populations. In contrast, IBMs provide great flexibility and detailed insights into population dynamics, primarily because they explicitly account for individual variation [24,25]. Although IBMs and MMs often produce similar results, particularly when the MMs account for aspects of variation, IBMs require substantially higher computational effort [26,27]. Therefore, matrix models provide a good compromise and allow studying structured populations with reasonable computational effort.

Conventional matrix models used for studying fish populations, also known as Leslie matrix models [28,29], consider only age classes. Although age is a natural demographic property in whitefish life history, vital parameters and management interventions often depend on body size [30–33]. A length-based model may therefore be more suitable for whitefish populations.

Here, we use a length-structured matrix model with temperature dependence and density dependence in growth and mortality to evaluate the effects of increasing habitat temperatures on the total biomass and catch by recreational anglers of a European whitefish population. A long-term (10 years) dataset of experimental gillnet catches was used to derive model parameters for the whitefish population of Lake Irrsee [34,35]. We further compare our modeling results to projections by simple regression models describing the correlation between catch and habitat temperature. We additionally assess the cost-effectiveness of the applied stocking strategy on the Lake Irrsee population and compare it to various other strategies with consideration of the fraction of invested money on small (i.e., 1 cm total length) and large (i.e., 10 cm total length) fish under constant and under continuously increasing temperature scenarios. Finally, we offer policy recommendations for stocking strategies of European whitefish under the aspect of climate change.

Material and Methods

We develop a process-based model to project the whitefish population of Lake Irrsee under different stocking and temperature scenarios. The resulting length-structured matrix model augmented with stochastic elements includes all relevant processes for population dynamics of whitefish, which are: temperature-dependent and density-dependent growth, survival, and reproduction.

Stocking strategies and catch by anglers are incorporated into the model through vectors of stocked and caught whitefish, respectively. Assuming different temperature scenarios, we project annual biomass and catches over a period of 50 years with different stocking strategies. Below, we briefly discuss selected points specifically. Details can be found in the supplementary material.

Sampling data

The pre-alpine Lake Irrsee, Austria ($\mathrm{N}\,47°\,53', \mathrm{E}\,13°\,18'$) is classified as an oligo-mesotrophic lake with a holomictic-dimictic mixing regime. Its maximum depth is 32 m and its surface area stretches over 3.6 km^2. European whitefish is the dominant fish species in Lake Irrsee and important for the local recreational fishery.

Since the year 2000, the whitefish population of Lake Irrsee is studied by means of gillnetting carried out annually in October (pre-spawning census; [34,35]). The overall catch amounted to 2,013 individual whitefish between years 2000 and 2009. Gillnet fleets with different randomized mesh sizes between 15 mm and 70 mm were assembled and set over night in part of the lake in 12to 15m depth.

Individual length (± 0.5 cm), weight (± 5 g), age, sex and ripeness of gonads were determined for all caught whitefish. Age identification was achieved by scale reading according to the method used by Devries & Frie [36] and Gassner et al. [34].

The examination of sex and ripeness stages according to Nikolsky (in: Ricker [37]) was done after dissection by classifying individuals into male, female, or juvenile and as spawners or non-spawners. Fresh eggs of mature female individuals were counted per unit weight in the year 2010 according to the gravimetric sub-sampling method described by Bagenal [38].

Total fish biomass in Lake Irrsee was estimated through simultaneously performed hydro-acoustic surveys in the open water area with two split-beam echo sounders in the year 2000 [39]. The population biomass of European whitefish was assumed to account for 60% of the total observed biomass.

Temperatures and oxygen concentration were available from water samples collected in $0, 2, 5, 8, 10, 12, 15, 20, 25,$ and $30\mathrm{m}$ depth at the deepest site of the lake on a monthly basis. Temperatures were measured in the field with a mercury thermometer and oxygen concentrations were determined in the laboratory according to the Winkler procedure [40]. Annual mean growth temperatures for European whitefish during the growth period from May to October were derived from temperature measurements in the suitable oxythermal habitat for coldwater fish (i.e., $\mathrm{O}_2 > 3\mathrm{mgl}^{-1}$and $T < 21.2$ °C; [41])

Spawning, eggs, and larvae

European whitefish reproduce in early winter and spawned eggs develop over the winter months till larvae hatch in spring [42–44]. We calculated the biomass of female spawners using the observed sex ratio, a sigmoid maturity function [33], and an allometric length–weight relationship. The average fecundity, that is, the average number of eggs per unit weight female fish, is estimated from our data and modeled as a stochastic variable. Finally, the number of hatching larvae, and thus the success of natural reproduction, is obtained from the effective fecundity, which is defined as the number of produced offspring that survives till hatching from the egg.

Survival is usually much lower for early development stages compared to larger fish, like in eggs and freshly hatched larvae [45, 46]. We assume egg mortality over the developmental period and larval mortality over the first four weeks of life to be much higher compared to mortality rates of larger whitefish (see supplementary material).

Density-dependent and temperature-dependent growth

Growth of a fish is depends primarily on size and is also affected by population density and environmental temperature. Small fish grow almost linearly and large fish grow according to a von Bertalanffy model toward an asymptotic length [47]. The asymptotic length depends on total biomass and therefore on population density via a Maynard Smith–Slatkin-type functional response [30, 48–50], while the von Bertalanffy growth coefficient depends on environmental temperature ([18, 51, 52]; see supplementary material for details). Asymptotic length and growth coefficient are related [17, 18], which makes the asymptotic length also indirectly dependent on temperature. We assume a lognormal distribution of monthly growth increments and allow growth to vary among individuals of the same length.

Natural and fishing mortality

Natural mortality of a fish is related to growth and environmental temperature [17, 54, 55] and therefore indirectly depends on population density. We estimated natural mortality through two different methods ([17,18]; see supplementary material) from density-dependent and temperature-dependent growth parameters. Additionally, we consider fishing mortality. Fisheries impose certain size limits which leads to selective removal of fish ofcertain lengths. We model this size-selective removal as a stochastic process. We assume a constant angling effort per unit time, which implies that the total catch is limited, and that total catch drops faster than linearly as abundance in the catchable size range decreases towards 0. We used catch statistics of the local angler association for parameterization of stochastic fish removal by anglers.

Stocking strategies

Currently, fisheries stock small whitefish (around 630,000 individuals of ~1 cm length with an individual price of €0.014) in March and larger whitefish (around 6,000 individuals of ~10 cm length with an individual price of €0.30) in September. This means that about 83% of the money invested into stocking is used for stocking small fish and the remainder for stocking large fish. To compare the cost-effectiveness, we investigate stocking strategies that allocate the same total amount of money in different ratio (thus, a stocking ration of 0.1 means 10% of the money is invested into stocking small fish etc.).

Temperature scenarios

We consider three different temperature scenarios (i.e., constant temperature, +1℃, and +2℃ over 50 years) The two scenarios with increasing temperatures are based on the observed temperature increase in surface waters of Lake Irrsee over the last decades (i.e., annual average with +0.9℃ and average of spring and summer temperatures with +1.9℃; [1]) and we also consider deep water warming and projected future temperature development of Austrian lakes described in Dokulil et al. [2] and Dokulil [3].

Results

We projected population biomass and anglers catch under changing annual habitat temperatures, investigating three basic temperature scenarios. We compared the predictions from simple regression models to our process-based model; we investigated the effects of increasing temperatures on biomass and catch; we analyzed the mechanism underlying the temperature effect; and finally assessed stocking strategies comprising introductions of small and large whitefish in different ratios.

Process-based model vs. regression models

Projections with the process-based model are shown for two different estimates of natural mortality (Pauly 1980; Jensen 1996), both resulting in qualitatively very similar predictions. We project annual catches (with a three year delay) as a function of growth temperature with our process-based model and extrapolate catches with simple regression models fitted to observations. The quadratic regression model agrees with the process-based model in that both project saturating catch at low growth temperatures. The exponential regression model agrees with the process-based model in that both project decreasing catches with increasing growth temperatures showing a non-linear pattern (although projected catches differ substantially). Quadratic and linear regression models project a complete collapse in catches for a relatively modest increase in growth temperatures similar to the collapse projected by the process-based model. In contrast, the linear and the exponential regression model also project high catch without saturation for low growth temperatures. No regression model shows qualitative agreement with the process-based model over the whole range of growth temperatures considered (Fig. 1).

Temperature effects

Using our process-based model we project changes in population biomass and catch by anglers over a period of 50 years under three temperature scenarios (Fig. 2.a). We find that population biomass and catch by anglers decrease with increasing temperatures. The effect is stronger when the temperature increase is larger. Our projections with Jensen´s estimate of natural morality show that increasing habitat temperature reduce biomass by about 2.6% (i.e., $-0.9\ \mathrm{kg\ ha^{-1}}$) and by about 4.4% (i.e., $-1.6\ \mathrm{kg\ ha^{-1}}$), respectively (Fig. 2.b), while catch decreases by about 24% (i.e., $-1.2\ \mathrm{kg\ ha^{-1}}$) and 45% (i.e., $-2.3\ \mathrm{kg\ ha^{-1}}$), respectively (Fig. 2.c). Our projections with Pauly´s estimate show that increasing habitat temperatures reduce biomass by about 4.3% (i.e., $-1.7\ \mathrm{kg\ ha^{-1}}$) and by about 7.9% (i.e., $-3.1\ \mathrm{kg\ ha^{-1}}$), respectively, and that catch decreases by about 26% (i.e., $-1.4\ \mathrm{kg\ ha^{-1}}$) and 48% (i.e., $-2.6\ \mathrm{kg\ ha^{-1}}$), respectively (not shown).

Underlying mechanism

Temperature has direct and indirect effects in our process-based model. The growth coefficient depends directly on temperature (Fig. 3.a) via a simple relation (see material and methods section and supplementary material). Since population dynamics in the model depends on growth, also the density-dependent parameters asymptotic length and survival probability are indirectly dependent on temperature. Increasing temperature increases the growth coefficient (Fig. 3.a) and decreases asymptotic length (Fig. 3.b) and annual survival (Fig. 3.c). Our projections show that increasing habitat temperature increase the growth coefficient by about 6.7% (i.e., $+0.02\ \mathrm{y^{-1}}$) and 12.4% (i.e., $+0.02\ \mathrm{y^{-1}}$), respectively, while asymptotic length decreases by about 2.9% (i.e., $-1.3\ \mathrm{cm}$) and 5.2% (i.e., $-2.3\ \mathrm{cm}$), respectively, and natural annual survival decreases by about 3.7% (i.e., -0.02%) and 6.7% (i.e., -0.04%), respectively. Our projections using Pauly´s estimate show that increasing habitat temperature increase the growth coefficient by about 6.7% (i.e., $+0.02\ \mathrm{y^{-1}}$) and 12.4% (i.e., $+0.05\ \mathrm{y^{-1}}$), respectively, while asymptotic length decreases by about 2.7% (i.e., $-1.2\ \mathrm{cm}$) and 4.8% (i.e.,

-2.1 cm), respectively, and natural annual survival decreases by about 4.6% (i.e., -0.03%) and 8.6% (i.e., -0.05%), respectively.

Stocking strategies

Stocking strategies, in our case, are expressed by the ratio of money invested into stocking small fish to the total amount of money invested for stocking. This includes the extreme cases where the money is invested either only into stocking small fish (corresponding to a stocking ration of 1) or only into stocking large fish (corresponding to a stocking ratio of 0). To assess the cost-effectiveness of stocking strategies for constant temperatures, we project population biomass and catch by anglers for different stocking ratios with a fixed investment budget. Different stocking ratios result in very different numbers of introduced fish, because large fish are substantially more expensive than small fish (e.g., in Lake Irrsee10 cm fish cost 21.4 times more than 1 cm fish). Our projections reveal that increasing the current stocking ratio of 0.83 increases population biomass after 10 years, and decreasing the current stocking ratio decreases biomass, while the catch remains nearly the same with a very inconspicuous peak at a stocking ratio of about 0.6(Fig. 4).

Mitigation of climate change

To evaluate how stocking strategies can be adapted to mitigate the effects of climate change, we project population biomass and catch by anglers over a period of 10 and 25 years for increasing habitat temperatures (+2℃ over 50 years; Scenario 3 in Fig. 2 and 3) and different stocking ratios. Compared to the projection with constant temperature (Fig. 4), population biomass and catch by anglers is generally lower. The catch, however, is now clearly maximized at lower stocking ratios of about 0.3 (Fig. 5).

Discussion

Whitefish stocks in cold Alpine lake ecosystems are affected through increasing temperatures due to climatic changes. Fisheries management of coldwater fishes commonly uses stocking to maintain available catches for recreational and commercial fisheries. To evaluate the often unknown effects of stocking on population dynamicsas well on the fishery itself, we have developed a process-based model of density-dependent and temperature-dependent population growth. Density dependence has been introduced in the growth parameter asymptotic length: higher population densities reduce asymptotic length [53]. Additionally, the effect of temperature has been integrated into the growth coefficient: higher temperatures lead to higher growth coefficients (depending on the temperature optimum for coldwater fish; [14, 41, 56]).

Natural mortality of whitefish has been derived from growth parameters and temperatures through two different methods [17, 18]. Both are considered to produce useful estimates when the growth coefficient can be derived accurately from population data and when adult life span is not exceptionally long [55]. We found that the simpler method proposed by Jensen [18], generally leads to higher estimates of natural mortality than the regression based model of Pauly [18]. Still, both methods produce qualitatively and quantitatively similar results in our model projections.

The parameterization of the process-based model is based on an empirical long-term data set of Lake Irrsee collected by annual gillnet samples and catch statistics. We have estimated initial biomass, growth parameters, fecundity, maturity and sex ratio directly from the data. Because of the importance of predation mortality in early life stages, we have modeled early life-stage mortality separately as a density-independent process. Nevertheless, reproduction is temperature- and density-dependent because of the relationship between adult size and reproduction efficiency (i.e., size-dependent maturation and size-dependent egg production). The optimal temperature range for whitefish growth, as well as egg and larval mortality, which were not available from field sampling, have been taken from literature. The sensitivity of our model to egg and larval mortality is high, which is in accordance to theoretical expectations that early life stages have a strong influence on population growth and consequently on recruitment to the fishery [45, 57, 58].

The assumed optimal growth temperature range (i.e., $T_{\mathrm{min}} = 2$℃, $T_{\mathrm{max}} = 22$℃) had also a great effect on the quantity of projected catches, whereas the decreasing trend with increasing temperature was robust. The minimal temperature for growth that we used in our model was very precisely evaluated by Siikavuopio et al. [59] who showed that whitefish grows at 3℃ but not at 1℃ water temperature. In contrast, the maximum temperature for growth is characterized only vaguely in literature and ranges from 13.5℃ to 22℃ [14, 56, 59–61] and it is also very likely that this term is species-specific as proposed by Ohlberger et al [62]. Consequently, the temperature at which a collapse of an actual fishery occurs may be different from the 13℃ at which it was observed in our model projections. To refine the prediction, the maximum temperature for growth needs to be assessed more accurately.

The strength of our model is the consideration of important life-history processes with respect to body size. Although simple statistical models showed similar trends of catches under a changing climate, the underlying mechanisms in population dynamics remain unclear, and consequently a process-based model is advantageous.

Our results clearly demonstrate that lower catches must be expected in whitefish fisheries with continuously increasing temperaturesin the future. Additionally, the process-based model reveals that lower catches are mainly due to accelerated growth of juveniles resulting in smaller sizes of adults and consequently lower recruitment into the established size-limit of the recreational fishery. We further found that population biomass decreases as a consequence of higher natural mortality. Modeling results for different stocking strategies indicate that this trend could be partly mitigated through stocking higher ratios of small fish. While changing stocking strategies cannot prevent a reduction in catch with increasing temperatures, stocking larger fish nevertheless seem to be more advantageous for the recreational angling fishery, insofar as it maximizes catch under the circumstances and thus angler satisfaction.

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Figure captions

Figure 1:

Catch predictions of our process-based model compared to simple regression models. Black solid lines show predictions of three regression models (linear, quadratic, and exponential) fitted to observational data of growth temperature and anglers catch, with a time lag of three years (black points; see text). Grey points and interpolation lines show predictions of our process-based models using two different mortality estimation procedures. All models capture the decrease of anglers catch with increasing temperatures. They differ in whether they allow a saturation of the catch towards low temperatures, and in whether they allow a collapse towards high temperatures and in how this collapse is approached.

Figure 2:

Increasing growth temperatures decrease population biomass and catch. Projections for three different temperature scenarios (a): constant temperature (black line), +1°C increase over 50 years (orange line) and +2°C increase over 50 years (red line). Population biomass of whitefish decreases only slightly with increasing temperature (b), while catch by recreational angling decreases substantially with increasing temperature (c). Grey shading indicates the initial stabilization period (see text).

Figure 3:

Higher temperatures affect growth and survival. Increasing temperatures (a) increase growth coefficients, (b) decrease asymptotic lengths and (c) consequently also reduce annual survival. Colors as in Fig.2.

Figure 4:

Stocking ratio affects population biomass more strongly than catch. For constant temperatures, solid bars show projected population biomass (black) and catch by anglers (grey) ten years after changing the stocking ratio (i.e., fraction of money invested in small fish) from the current stocking ratio in Lake Irrsee of 0.83.

Figure 5:

With increasing temperatures catch is maximized at lower stocking ratios. For increasing temperatures (+2°C over 50 years; scenario 3 in figure 2 and 3), panels show projections of population biomass and catch by anglers after (a) 10 years and (b) 25 years after changing the stocking ratio from the current stocking ratio (see Fig.4).

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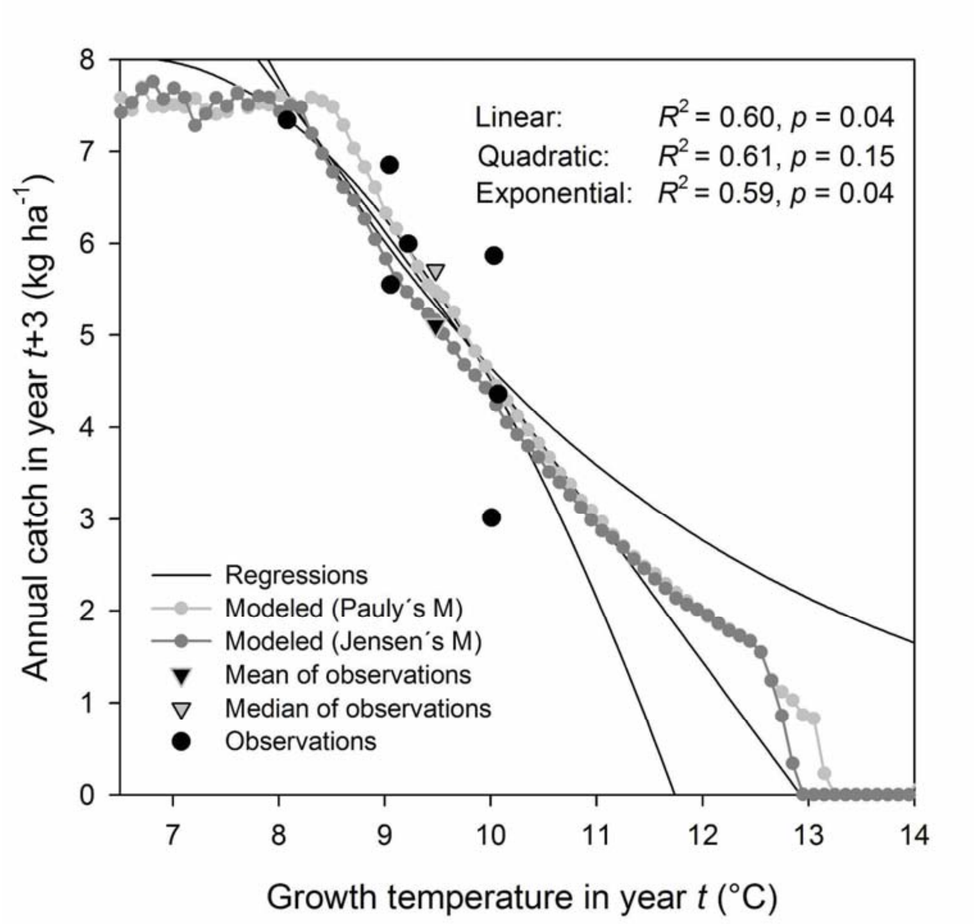

Figure 1:
Catch predictions of our process-based model compared to simple regression models. Black solid lines show predictions of three regression models (linear, quadratic, and exponential) fitted to observational data of growth temperature and anglers catch, with a time lag of three years (black points; see text). Grey points and interpolation lines show predictions of our process-based models using two different mortality estimation procedures. All models capture the decrease of anglers catch with increasing temperatures. They differ in whether they allow a saturation of the catch towards low temperatures, and in whether they allow a collapse towards high temperatures and in how this collapse is approached.

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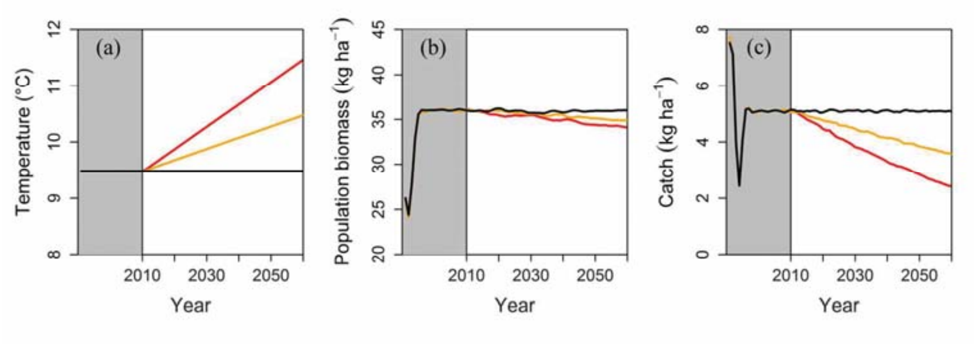

Figure 2:
Increasing growth temperatures decrease population biomass and catch. Projections for three different temperature scenarios (a): constant temperature (black line), +1°C increase over 50 years (orange line) and +2°C increase over 50 years (red line). Population biomass of whitefish decreases only slightly with increasing temperature (b), while catch by recreational angling decreases substantially with increasing temperature (c). Grey shading indicates the initial stabilization period (see text).

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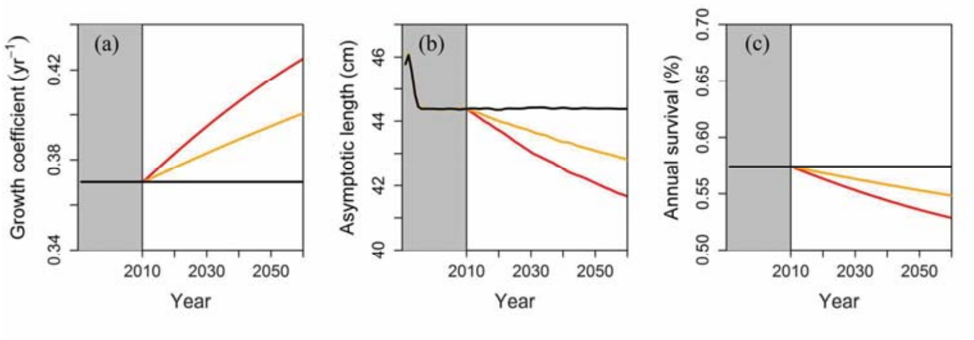

Figure 3:
Higher temperatures affect growth and survival. Increasing temperatures (a) increase growth coefficients, (b) decrease asymptotic lengths and (c) consequently also reduce annual survival. Colors as in Fig.2.

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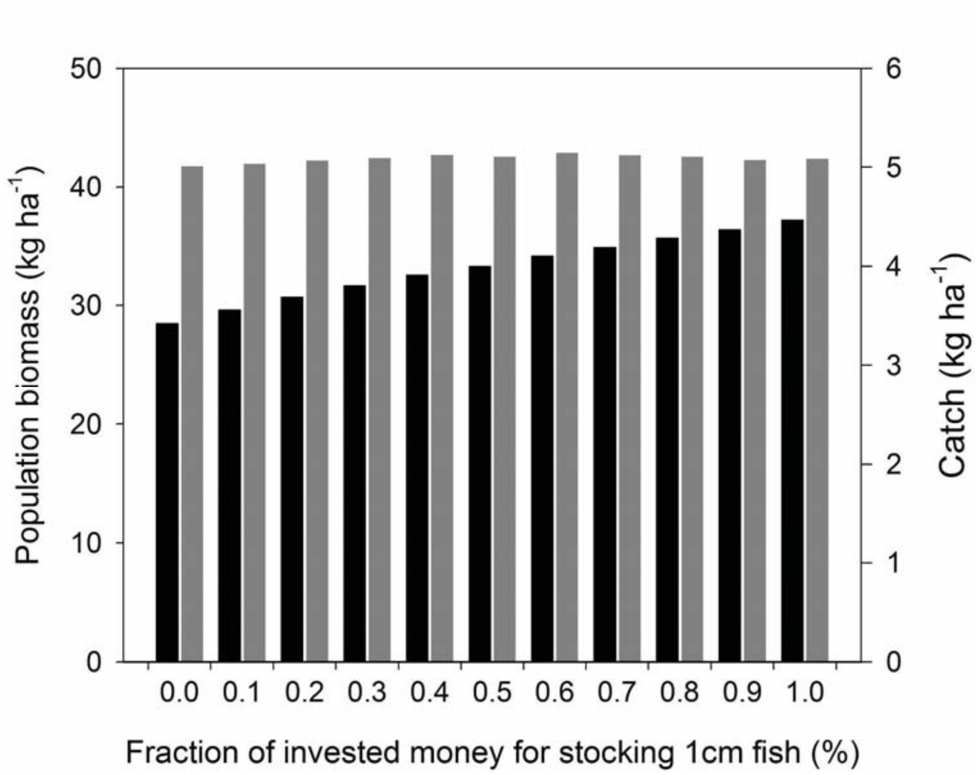

Figure 4:
Stocking ratio affects population biomass more strongly than catch. For constant temperatures, solid bars show projected population biomass (black) and catch by anglers (grey) ten years after changing the stocking ratio (i.e., fraction of money invested in small fish) from the current stocking ratio in Lake Irrsee of 0.83.

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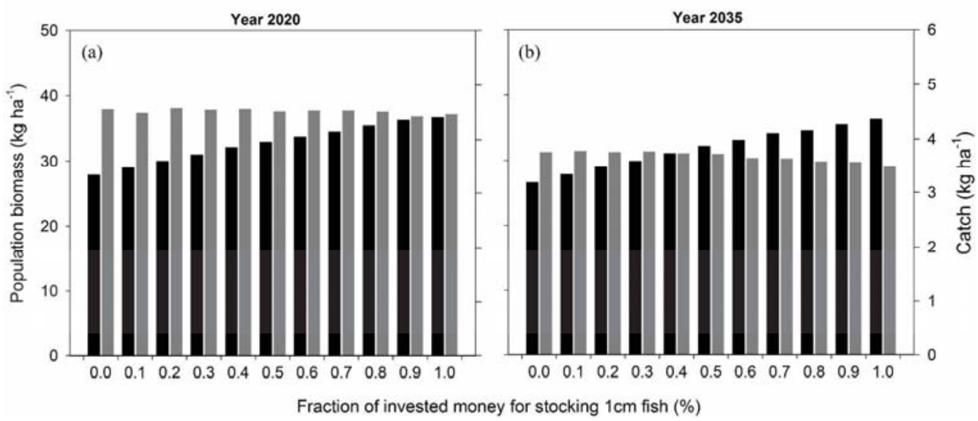

Figure 5:
With increasing temperatures catch is maximized at lower stocking ratios. For increasing temperatures (+2°C over 50 years; scenario 3 in figure 2 and 3), panels show projections of population biomass and catch by anglers after (a) 10 years and (b) 25 years after changing the stocking ratio from the current stocking ratio (see Fig.4).

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Table 1: Parameters used in the length-structured matrix model.

Parameter	Symbol	Unit	Value	Reference
Mean annual growth temperature	T_g	℃	9.48	Irrsee data
Minimum growth temperature	T_min	℃	3	Siikavuopio et al. 2010
Maximum growth temperature	T_max	℃	22	EIFAC 1994; Stefan et al. 1995
Optimal growth temperature	T_opt	℃	14.1	Casselman et al. 2002
Fecundity (eggs per mass)	f	g^{-1}	19.4 ± 1.63 SD	Irrsee data
Egg mortality	q	d^{-1}	0.06	Wahl &Löffler 2009
Sex ratio (female/male)	r	1	1	Irrsee data
Asymptotic length (initial value)	L_∞	cm	45.09	Irrsee data
Growth coefficient (initial value)	k	y^{-1}	0.37	Irrsee data
Age offset	A_0	y^{-1}	-0.65	Irrsee data
Whitefish biomass in year 2000	B	$\mathrm{kg\ ha}^{-1}$	30.98	Irrsee data